

THE STRUCTURAL CONSEQUENCES OF MODIFI-
CATIONS OF THE DEVELOPMENTAL RATE
IN FISHES, CONSIDERED IN REFER-
ENCE TO CERTAIN PROB-
LEMS OF EVOLUTION



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I. THE CONSEQUENCES OF MODIFICATIONS OF THE DEVELOP-
MENTAL RATE ON GROWTH AND ON DIFFERENTIATION

WHILE engaged in a series of studies¹ undertaken to determine the relation of environment to variation in fishes, the writer has been led to interpret certain physiological phenomena as significantly and factorily involved in structural evolution.

The central interpretation, the validity of which seems substantiated by the evidence embodied in this paper, is that those conditions, whether "external" (direct; individual) or "internal" (genetic; racial), which alter the rate of development,² affect the differentiation aspect of development in the same direction as the growth aspect. Conditions which accelerate the development rate accelerate and accentuate the differentiating tendencies, as well as the growth tendencies. Retarding conditions, on the other hand, retard and reduce both differentiation and growth.

As an example of this developmental phenomenon, the relation of changes in the rate of general development of fishes to the specific development of the scales may be cited. In the cases which have been studied, as the her-

¹ A number of these studies are not yet published. Those which have already been printed are referred to in the list of literature cited.

² The general influence of temperature on developmental rate is too well known to require special discussion here. Reference may be given, however, to papers on this subject by Johansen and Krogh (1914), and by Krogh alone (1914).

ring (Heincke, 1898; Ehrenbaum, 1909) and a number of cyprinids, percids and blennioids (Hubbs, Ms), it has been found that the formation (differentiation) of the scales is retarded or accelerated by those conditions which respectively delay or hasten growth. As a consequence, the scales do not appear until a larger size has been attained in slow-growing races or species than in the case of fast-growing forms.

The relation of growth and differentiation is evident in the main course of normal development. During the segmentation of the ovum there occurs a great multiplication of cells, but practically no growth; concomitantly, little differentiation. Subsequently the growth rate, as measured by proportionate increase, assumes its highest value. At the same time differentiation is enormously accelerated—more so relatively than the growth, for at given stages in early development the proportionate completeness of differentiation is greater than that of growth. Later in development the gradual decline in proportionate growth increase per unit time is accompanied by a decrease, relatively even greater, in the differentiation rate. These relations were discussed, from a different viewpoint, by Minot (1908).

In the present connection the well-known control by the thyroid increscent over both rate of metabolism and the rate of differentiation³ (especially metamorphosis) should be considered. The effects of low temperatures in greatly retarding metamorphosis (*i. e.*, condensed differentiation) without having any apparent effect on the thyroid gland (Uhlenhuth, 1923, p. 318, and subsequent papers) seemingly fall into line with a very general tendency and do not appear to require the postulation of a "releasing mechanism" or "excretor substance."

In agreement with this central interpretation that conditions modifying the development rate affect differentiation in the same direction as growth, it apparently usually holds true that accelerating conditions more

³ For a very recent discussion of this problem, see Budington (1925).

quickly, more abruptly and to a greater degree affect the general slackening of the growth rate with age than do conditions retarding the development rate. Thus Lehenbauer (1914) found that the rapid initial rate of growth of plant seedlings under high temperatures is not long maintained, whereas the slow initial growth under low temperatures is maintained even under prolonged exposure. Similar relations often if not in general hold for the whole life-cycle of fishes. Pütter (1920) recently made a strained effort to explain this situation in terms of the "simplest possible physico-chemical phenomena." His treatment of the subject was largely deductive, and in deriving his formulas for the computation of growth at different temperatures he made a number of assumptions which seem unwarranted. As a culmination of his deductive mathematical analysis, he arrived at the surprising conclusion that a positive growth increases up to a certain point (the greatest size being attained at 0° C.), beyond which a negative growth period obtains, causing the animal to return, death not intervening, toward a zero size.

Pütter's deductive analyses do not seem to invalidate the following interpretation of the reason why retardation of growth with age occurs more quickly and is more abrupt and extensive under accelerating than under retarding conditions of development. Under any conditions which accelerate development, the early growth is fully accelerated, by reason of the fact that inhibitory tendencies have not yet been brought into effective action. The later growth, on the contrary, is relatively very extensively retarded, because the development of inhibitory tendencies, like other controls of differentiation, is also hastened and accentuated. The general growth inhibitions, as is well known, often are associated with the ripening of gonads, the attainment of maturity being marked by a cessation of growth in warm-blooded animals, and usually by a sharp decline in the growth rate in the case of fishes and other animals exhibiting indeterminate growth. Accelerating conditions hasten the

inception of maturity and the associated decline in growth rate.

The abrupt and extensive retardation of growth under accelerating conditions of development explains the general observation that fishes of cold or saline waters usually attain a larger size than do individuals or races of the same species inhabiting warm or brackish water, or both (see Möbius und Heineke, 1883). This principle usually holds true despite the great shortening of the growing season in northern waters⁴, a condition which is probably responsible for nearly all the apparent exceptions to the general rule. The exceptions are spoken of as apparent, because they would not appear as such if the growth were expressed on a *per diem* rather than on the physiologically less significant seasonal basis. As a very general rule the warm-blooded vertebrates also increase in size toward the north (Allen, 1871 to 1877).

This reversed action of differential acceleration on early and on late development apparently applies not only to the entire development, but also to any stage thereof which involves growth and is brought to a close by inhibition. Thus it is very generally true that, in those individuals or races of fishes which show an accelerated embryonic development, the addition of somites—which is practically synonymous with the growth of the embryo—proceeds much faster than in those individuals or races of the same species subject to or exhibiting a relatively retarded development, but the increase, like that of growth in general, terminates relatively sooner and more abruptly. As a final consequence, warm or brackish water representatives have as a very general rule fewer vertebrae than do individuals or races of the same species inhabiting water of lower temperature or higher salinity.⁵

⁴ In northern Michigan, for example, Dr. C. W. Creaser and the writer found that the growing season of fishes scarcely extends beyond the four months of June, July, August and September.

⁵ This phenomenon is the special subject of a series of papers published (Hubbs, 1922, 1924a, 1925) or being prepared by the writer. Space will not permit the discussion here of the data and literature bearing on this problem.

Modifications in segment number of fishes may also be associated with differences in development rate, which, unlike those just discussed, are not interpretable as metabolic adaptations to the environment. For example, the retardation of development brought about by the deposition of an unusually large amount of yolk in the ovum often is correlated with a great increase in segment number. Thus most elasmobranchs and chimaeras as well as many genera of teleosts, as, for instance, *Synbranchus*, have very large eggs and very numerous segments; a review of the data will be presented in a future paper. A protracted development associated with viviparity, in the Embiotocidae or viviparous perches of California (Eigenmann, 1894a; Hubbs, 1921c), is correlated likewise with an increase of vertebral number. Similarly, the slowing down of development, conditioned by the insertion into the life-cycle of that peculiar larval-postlarval adaptation to pelagic life which finds its extreme expression in the leptocephalus stage of the eels, seems to bring about an increase in the number of segments. Such larvae or postlarvae—inordinately elongated and compressed creatures having the muscle replaced by gelatinous tissue—contrast sharply with the compact, muscular and often spined or armored early stages of fishes having an accelerated larval development accompanied by a low number of segments. An examination of the extensive literature dealing with the early development of fishes indicates that probably all the numerous spiny-rayed fishes possessing the characteristically low and basic vertebral formula, $10 + 14 = 24$,⁶ almost certainly all with the total number reduced below 24, and many with the number but slightly increased beyond 24, pass through a markedly abbreviated development.⁷ These cases of cor-

⁶ An excellent discussion of the evolutionary significance of this basic vertebral formula of the acanthopterygian fishes is given by Boulenger (1905).

⁷ The limits of the present paper do not permit a detailed discussion of the extensive literature and data bearing on the early development of fishes. It is planned to deal with the problem in another paper.

relation between rate of development and the number of segments are far too numerous and clear-cut to be passed by as coincidences.

The relation between differential rate of development—whatever its basis may be—and the number of vertebrae eventually produced becomes particularly apparent in the comparison of related forms. Thus the spring-spawning races of the European herring have fewer segments than the autumn-breeding types, and a more accelerated development (Heincke, 1898; Ehrenbaum, 1909). Similarly, the race of anchovy inhabiting the brackish waters of San Francisco Bay has fewer vertebrae and a less protracted development than the typical *Engraulis mordax* of the adjacent ocean coast of California (Hubbs, 1925). The European eel develops more slowly than the American species, and has more segments (Schmidt, 1922). *Argentina silus* has more segments than *Argentina sphyraena*, and a more protracted early development (Schmidt, 1906). *Agonus cataphractus*, with 36 vertebrae, has a much less extended development than *Leptagonus decagonus*, which has 45 vertebrae (Schmidt, 1908). Many other cases show a like correlation between rate of development and number of segments.

Those fishes which pass through a protracted development usually show an extenuation not only of growth, but also of those age differentiations in form which result from the differential rate of growth in various parts of the body. They usually have, for instance, proportionately shorter heads and smaller eyes than related forms (or individuals) of more accelerated development, the normal age changes in the proportions of these parts being carried to a farther degree. These changes take place, whatever be the underlying cause of the retardation in development, whether the coldness or salinity of the water, or an increase in the amount of yolk material in the egg, or a gelatinous specialization of the early stages. The changes seem to occur when the basis of retardation is individual, as well as when it is genetic.

Fishes of retarded development frequently show, also, an increased development of those modifications of the skin, such as cirri, bony plates and spines, which appear at a relatively late stage.

This increase in differentiation of form and of dermal structures in the later part of development, under retardation conditions, is not merely proportionate to the extenuation of growth rate; it is evident sooner in reference to general development. Thus not only at the larger sizes attained, but also at comparable sizes, the head and the eye are proportionately reduced. This general phenomenon lines up with the central interpretation that differentiation is affected in the same direction as growth by conditions altering the development rate. In this case the action of differentiation controls (inhibitions) is obviously hastened and accentuated in accelerated development.

The decrease in the late differentiation of fishes of accelerated development was appreciated as early as 1883 by Möbius and Heincke, who wrote (1883, p. 184):

Bei marinen Arten wirkt die Anpassung an das Brackwasser in einer ganz bestimmten Weise verändernd und zwar bei allen Arten in gleicher Weise. Schon bei der Charakteristik der nordöstlichen Ostsee sind Andeutungen hierüber gemacht.

1. Die Brackwasserrassen sind kleiner, ihr Rumpf ist höher, die Bewaffnung des Körpers mit Stacheln und ähnlichen Hautbildungen ist schwächer. Letzteres zeicht sich namentlich bei dem kleinen ungepanzerten, kurzstacheligen *Gasterosteus leiurus* im Gegensatz zu dem grossen, gepanzerten, langstacheligen *trachurus* ferner bei den in Brackwasser lebenden Individuen von *Cottus scorpius*. Noch besser werden wir diese Thatsachen ausdrücken, wenn wir sagen: Die Brackwasserrassen werden auf einen jugendlicheren Stadium geschlechtsreif, als die Salzwasservarietäten derselben Art. Nach den Erfahrungen am Heringe zu urtheilen, ist eine Hauptursache dieser Verschiedenheit die schnellere Entwicklung der Eier und der ausgeschlüpften Brut im Brackwasser, welche wiederum durch physikalische Verhältnisse, wie geringe Tiefe, höhere Temperatur, intensiveres Licht, geringeren Salzgehalt an den Laichplätzen und schwachere Bewegung des Wassers bedingt sein wird.

The data used as the basis of these principles were in part elsewhere published by Heincke, in his classical study on the races of the herring (1898), in a paper on

the Gobiidae and Syngnathidae (1880), and one on *Gasterosteus* (1889). Rutter (1896), Regan (1909), Snyder (1908) as well as Heincke, have remarked on the weak development of armature and spines in the freshwater forms of *Gasterosteus*, and have observed that changes which take place from the north to the south on the one hand, and from the sea into fresh-water on the other hand, are similar. Roth (1920) also noted a southward decrease in the number of plates in *Gasterosteus* and found that the plates progressively lost are the last ones ontogenetically developed, those first formed being racially most permanent.

In the most extensive racial investigation of fishes ever undertaken, Johannes Schmidt (1917a, 1917b, 1918, 1920, 1921; see also Smith, 1921) has found that a decrease in form differentiation and particularly in segment number of *Zoarces viviparus* generally takes place from the ocean into warmer and brackish fjords, and that the differences, although genetic, may also be experimentally altered to a slight degree^s.

The writer has found that most of the cottoid fishes of the open California coast show a gradual decrease toward the south in size and in form differentiation as well as in segment number. This case is of interest in showing that these modifications may be determined by changes of temperature as well as of salinity (see Huntsman, 1919), or by the combined action of both factors.

In the Atherinidae modifications similar to those observed in general have been found, a reduction in segment

^s The individual differences induced by Schmidt were of the opposite environmental correlation as compared with the racial differences. Individuals brought from the ocean outside into a fjord, and kept confined in live-boxes, produced offspring having a number of segments slightly (but significantly) lower, not higher, than either their parents or the mean race to which they belonged. In other words, water conditions which ordinarily induce accelerated development were here associated with such results as are usually produced by retarded development. But in this case the imprisonment of the viviparous fishes in the live-boxes may have reduced the metabolic activity of the mother and hence the developmental rate of the young. In this way an increased number of segments might have been induced.

number or in differentiation of form taking place toward fresh-water (Roule, 1902, 1903a, 1903b), toward the south in the Northern Hemisphere (Kendall, 1902; Hubbs, 1918; Jordan and Hubbs, 1919, p. 57-58), and toward the north in the Southern Hemisphere (Jordan and Hubbs, 1919, p. 15, 17, 66). In an Australian fish, *Retropinna*, in which McCulloch has found that similar differences occur, the variation is similarly in the opposite actual direction to that observed in the Northern Hemisphere, but in the same direction in temperature gradient. Many other instances of a confirmatory nature might be cited. A more extended discussion of the ichthyological data bearing on these problems will be presented in other papers.

APPARENTLY CONTRADICTORY CASES

Certain apparent exceptions to these general variational trends have been stressed by certain authors. Most such cases are those in which the environmental correlation seems to be the opposite of that admittedly usually shown. These require discussion at this time.

Schmidt has presented evidence to show that the inherent properties of the organism play a rôle of greater importance than the environment in such minor evolutionary processes as are here being discussed. Two of the instances cited by this author involve the number of segments of the clupeoid fishes. While it is generally obvious that the number of segments in *Clupea harengus* decreases toward warmer and less saline waters, Schmidt points out that the White Sea herring is characterized by an incompatibly low number. But this race seems to belong to another species, the Pacific herring (*Clupea pallasii*), as indicated by us, and it has more vertebrae than the British Columbia race of that species, which in turn has more segments than the California form (Hubbs, 1925). Again, Schmidt points out that the related sprat (*Sprattella sprattus*) in the Baltic region seems to vary in a direction opposite to that there exhibited by *Clupea*

harengus. But later work has not confirmed this evidence: probably annual variations exceed the geographic in the sprat (see data in Fage, 1920).

Schmidt furthermore lays much stress on the fact that the variations in *Zoarces* are not perfectly correlated with environmental factors, and dismisses, we think without good reason, the possible differential action of varying combinations of temperature and salinity. As a whole, however, Schmidt's elaborate data on *Zoarces* show conclusively that the segments decrease in number toward relatively warm and brackish water. As the evolution process seemingly involves the parallel selection of mutations, the surprise is that the relation of the characters of the races of *Zoarces* to their respective environments is as definite and close as Schmidt has shown it to be.

Cox (1923) has lately shown that a stickleback, *Apeltes quadracus*, shows an increase in the number of dorsal spines in the portions of the Gulf of St. Lawrence characterized by reduced salinity and increased temperature. This variation appears to have the opposite environmental correlation to that shown by other fishes in the same area. Cox (1903) earlier indicated that four species of flounders all showed in these shore waters a decreased number of fin rays and vertebrae as compared with their truly marine representatives, and Lea's data (1919) indicate that a similar trend of variation is shown by the herring in the same waters.

Certain fresh-water fishes show a decreased rather than an increased number of rays, in one of the vertical fins, in water of reduced temperature. Thus Schmidt (1919a, 1919b) has shown that the number of dorsal rays of the viviparous poeciliid *Lebistes reticulatus* is reduced in fishes developed in cold water. Despite this individual modification, small differences in ray number were found to be inherited. In the case of two related fishes, both of Middle America, *Pseudoxiphophorus bimaculatus* and *Priapichthys annectens*, we have recently shown (1924b)

that the number of dorsal rays decreases from the *Tierra Caliente* to the much cooler mountain streams. In an American minnow, *Notemigonus crysoleucas*, a somewhat similar variation is shown; in this case, however, involving the anal fin: the number of anal rays gradually decreases, in the average, from 15 to 11, in passing from Florida to Minnesota (Hubbs, 1921a). More extensive data, now at hand, emphasize the gradual nature of this variation, a decrease of one ray taking place each four hundred miles. The lines formed by joining localities with an equal ray number agree remarkably well with the spring isotherms, even including the southward dip in the Appalachian Mountains. A somewhat similar though much less regular correlation between temperature and anal ray number perhaps lies at the basis of the remarkably wide geographical variation exhibited by the Northwestern American minnow *Richardsonius* (for data see Eigenmann, 1894b, 1895; Gilbert and Evermann, 1894). In all these cases the exceptional variational trend seems to involve only the one fin, not the number of vertebrae, or other characters. No explanation of such cases can be offered now.

Another alleged instance of reversed environment correlation in such variations is that of the crustacean genus *Chiridothea*. Ekman (1919) has claimed that this "relict" form shows a character-gradient from salt water to fresh water exactly the opposite of that exhibited by other relict crustaceans. *Mysis oculata*, *Gammaracanthus loricatus* and to a lesser degree *Pontoporeia affinis* suffer a decrease in form differentiation in the salt-water to fresh-water series. The *Chiridothea*, on the other hand, is held to exhibit, in the same series, an increase in form differentiation, the adult being more extreme than the adult of the marine type, rather than, as in the other cases, resembling the young of the marine form. It must be noted, however, that there is reason to believe that the marine species cited (*sibirica*) is not, as Ewman claims, the "Stammform" of the brackish and fresh-water species

(*entomon*). The great differences in the size of the lateral expansions of the thoracic segments and in the shape and armature of the telson, exhibited in the young from the brood pouch, suggest that these species are not very intimately related: in these respects the young diverge more than the adults. Such being the case, the propriety of uniting these species into a single form-series may legitimately be challenged.

It is evident that some of the cases discussed above are not valid exceptions to the general principle under discussion. On the other hand, it is quite as clear that exceptions do exist, and in many other instances the correlation of characters with environmental factors is either lacking or highly imperfect and irregular. Indeed such principles can not be expected to be of invariable application. It seems quite safe to conclude, however, that the later differentiations in form and structure are in general carried farther under retardation conditions of development than under acceleration conditions.

II. THE BEARING OF THESE PHENOMENA ON SOME PROBLEMS OF EVOLUTION

(a) *The Problem of Adaptation*

As already indicated, modifications in the rate of development may entail definite structural changes. These modifications, when exhibiting a definitive environmental correlation, seem best interpretable as physiological adaptations. The adaptations may or may not be genetic: when direct, individual and external, the adaptation would be explainable in direct physiological terms; when indirect, racial and internal, the adaptation might well be regarded as the genetic modification of a developmental factor—the selection, perhaps, of a metabolic mutation. The adaptation would involve the genetic retardation of the developmental rate in those races habitually subjected to such environmental factors as individually retard development; or, the genetic acceleration of the developmental rate in those races ordinarily surrounded

by media which induce accelerated development in the individual. Thus subjection to waters of low temperature and high salinity either directly and individually, or indirectly and genetically, induce a retardation of development in fishes. The effect of either higher temperatures or decreased salinity is in the opposite direction. In either case the development modification is correlated with definite structural changes.

In other instances the modification of early physiological activity and developmental rate and the corresponding structural consequences have a basis in genetic changes in the amount of yolk in the egg or in the character of the tissues of the larval stage. In these cases the relation of the adaptation to changing environmental factors is at once obscure and indirect. Such adaptations meet primarily developmental rather than environmental needs.

The structural consequences of alterations in developmental rate involve the number of vertebrae, scales and fin-rays, the proportions, the development of dermal outgrowths, etc. These changes are often slight, only to be determined by statistical means, or they may be large. Most structural modifications of this type have usually been interpreted as being without adaptive significance, and partly on this basis, systematists in general hold that characters most serviceable in classification are of the non-adaptive type (see for instance Jordan, 1906). But many such modifications seem to be the direct consequences of physiological adaptations. Morgan (1923, 1924) has lately suggested, from a standpoint of genetics, that many apparently non-adaptive structural features may be produced by adaptive physiological modifications.⁹ The rôle of adaptation in evolution is probably more extensive than it has generally been held to be, in recent years.

⁹ Julian Huxley advanced this point of view, obviously in terms similar to those adopted in the present paper, in 1922 (see *Nature*, Vol. 110, No. 2770, December 2, 1922).

(b) *The Problem of Speciation*

The structural consequences of differential rate of development, as indicated in the foregoing discussions, probably comprise a considerable proportion of the characters differentiating local races among fishes, and perhaps many of the distinctive features of races in other groups of animals.

(c) *The Problem of Degeneration*

The interpretation of certain types of structural evolution as the definitive consequences of physiological mutations, if valid, render more definite our conceptions of the processes involved in evolutionary degeneration.

Evolutionary degeneration resulting from accelerated development is not usually if ever very extensive, although frequently evident, and perhaps quickly and readily brought about. Degeneration with this basis seems to involve chiefly the elimination of the final stages in differentiation of form and of dermal outgrowths, such as cirri, bony plates and spines. This elimination, as already stated, is the apparent consequence of the advancement and accentuation of the effective inhibitions. Degenerate forms so produced, if indeed they may legitimately be so named, are merely juvenile in their characters. Instances of such degeneration have already been given.

Degeneration correlated with decreased physiological activity and retarded development is in contrast apparently less readily and quickly consummated, but may be much more extensive, involving the elimination of final stages of early differentiations, these as a whole being more fundamental and extensive and more numerous than the late differentiations. This elimination is apparently the result of the parallel effects of retardation on differentiation and on growth. The appearance of the differentiations may be so greatly delayed as to be carried beyond the limit of the normal life-cycle. More frequently, however, their appearance is only delayed until

a time when conditions of general size, thickness of skin or ossification of bone, etc., preclude further differentiation.

Conspicuous examples of such degeneration correlated with retarded development, involving the retention of embryonic (as opposed to juvenile) characters, are to be found among the fishes. Mention may be particularly made of the retention of an open lateral line tube in fishes of exceedingly slow development, as the Chimaeridae and certain deep-sea teleosts, of a partially heterocercal caudal fin in the salmonid and coregonid fishes, of a semi-cartilaginous skull in the same and other groups. In all these cases the process of differentiation remains uncompleted in the adult. Similarly, when the squamation remains incomplete in the adult of forms with retarded development, those scales which are first lost in degeneration are those last formed in normal ontogeny. In those cases in which differences in completion of squamation appear within the species, the relation between the elimination of the final stage in scale formation and the retardation in development is particularly evident. It has been found, for instance, that in the more slowly developing races of several darters and a minnow, that the scales occasionally fail to cover the nuchal region, which is the last to be scaled over in ontogeny. In a Pacific coast blenny of retarded development, *Anoplarchus purpurescens*, in which scales never develop at all on the trunk, the forward extension of the scales is greater to the southward than to the northward¹⁰.

Degeneration resulting from altered developmental rate, it thus appears, involves the elimination of final stages in development, this being done in such a way that accelerated development involves the retention of juvenile features, while retardation involves the retention of embryonic characters. Degeneration of this type, as here interpreted, does not primarily nor necessarily involve

¹⁰ A fuller account of both these instances will appear later in other papers.

any direct genetic loss, but involves physiological adaptations which preclude the completion of certain ontogenetic processes.

(d) *The Problem of Progressive Evolution*

It is indicated in the foregoing section that the rôle of physiological adaptation is apparently not limited to the racial elaboration of the ends of evolutionary lines, apparently entering also into the process of extensive degeneration. It remains to be considered whether these physiological adaptations may be interpreted as significantly involved in progressive evolution.

An accelerated development, as pointed out in earlier parts of the paper, results in emphasis of the early differentiations, which are the most important in determination of the most essential characters of the adult. Obviously, however, the increase of differentiations must soon reach a genetic limitation, for all definitive differentiations must have a genetic basis. But acceleration may furnish a condition receptive to the introduction of new differentiations originating by mutation—thus contrasting with retardation, which might mitigate against the introduction of new differentiations. In agreement with these interpretations we find that those fishes which have a rapid development, as contrasted with those having a slow development, in general show a relatively higher degree of differentiation and specialization.

Physiological adaptations, which are probably the chief bases of differential rate of development, appear therefore to be significantly, although probably indirectly, involved in progressive evolution.

The evolutionary consequences of physiological adaptation on these assumptions would be analogous to those of natural selection. They apparently do not primarily or directly involve the origin of variations, but provide a means for their fixation and perpetuation. We should not overlook the possibility, however, that a high rate of metabolic activity may in some way lead to increased production of new heritable variations (mutations).

(e) *The Problems of Phylogeny*

Extensive degeneration, involving the retention of embryonic features, has here been interpreted as often a consequence of greatly retarded development. If this interpretation is valid, it follows that this phenomenon presents a means of testing whether simplicity of structure in a given group is a primitive or a secondary feature. The test would involve determining whether the development is or is not greatly retarded. For instance, the excessively slow development of the salmonoid fishes adds weight to the interpretation of the semicartilaginous skeleton, the partially heterocercal tail, etc., as secondary features, and to the consequent allocation of the group well within the teleost series, rather than between the ganoids and the teleosts. In this case, paleontological evidence is strongly confirmatory of the interpretation of relationships here made.

If the interpretations advanced in the previous sections of this work are valid, it would further follow that we have in the cases discussed a key to the determination of the direction and possible reversibility of the evolutionary processes involved. It appears probable that evolution of structure and form as conditioned by the modification of developmental rate through physiological adaptation or otherwise, may proceed in either a given direction or in the opposite direction (for example, either toward or away from a juvenile condition). Thus the southern derivatives of northern types of fishes are usually modified in the same general features as are the northern representatives of warm water types, but in the opposite direction.

It seems true also that structural evolution controlled by alterations in developmental metabolism is reversible. This possibility has not been considered by certain authors, as Smitt (1886, 1895, 1901a, 1901b) and Fage (1911), who have attempted to postulate the direction of speciation, nor by Jordan (1891, 1893) or Boulenger (1905) in their discussion of evolutionary changes of seg-

ment number. Thus we find that northern types of fishes which already have assumed such characters as are usually associated with and probably determined by a retarded development, become racially modified in the opposite direction after having reentered bodies of water which condition an accelerated development. The change is toward the original characters of the warm water ancestors of the northern types. The case of *Zoarces*, so elaborately investigated by Schmidt (1917-1921) is particularly clear. The typical basic race of the North Atlantic waters is characterized by features of form and proportions and the high number of segments associated with cold-water conditions. The numerous fjord races obviously evolved from this ocean race, and, living in water of increased temperature and decreased salinity, show modifications in form and proportions which slightly approach the characters of the more typical spiny rayed fishes of warm waters, from some one of which the zoarcid fishes must have sprung. The fjord races also show consistently a decrease in the number of vertebrae, which again marks a reversion toward the original warm-water ancestor of *Zoarces*.

This reversibility of such structural evolution as is determined by physiological adaptation would indeed be expected, if the interpretations of the present paper are valid. If alterations of developmental rate, as here assumed, determine certain definite structural changes, then a reverse metabolic adaptation would induce reverse structural changes. It might be expected that the reversibility would be very close and exact for the smaller evolutionary changes, as the loss of characters due to changed rate of development seemingly involves inhibitory actions of some kind, rather than, necessarily, genetic losses. A reverse metabolic mutation might automatically eliminate the inhibition, and permit the remanifestation of characters temporarily concealed along the phyletic line.

The strong probability of evolution leading either toward or away from the development of juvenile charac-

teristics in the adult, and of the process being reversible, makes it appear quite improbable that the biogenetic law applies in these cases. Of two related races or species, the one possessing characters diverging the less from the juvenile condition is not necessarily more primitive than the other or ancestral to it, as Smitt has consistently held in his fish studies (1886, 1895, 1901a, 1901b). The more juvenile of the two types, as for instance any of the fjord races of *Zoarces viviparus* (investigated by Schmidt), or of the similar fjord or estuarine representatives of many other ocean species of fishes, is in reality probably more frequently derived from, than ancestral to, the marine type which diverges to a greater degree from the juvenile condition. The biogenetic principle perhaps can not be applied at all to such evolutionary processes as are discussed in the present work.

III. SUMMARY

The central interpretation advanced in this paper is that either individual or racial modifications of the developmental rate affect the differentiation aspect of development in the same direction as the growth aspect. Conditions which accelerate the developmental rate accelerate and accentuate the differentiating tendencies as well as the growth tendencies. Retarding conditions operate in the opposite manner. This relation of growth and differentiation is evident in the course of normal development.

Accelerating conditions hasten growth in the early stages, but later bring about a slackening of the growth rate, probably because of their accentuated action on growth inhibitions. Retarding conditions cause a protraction of the early growth, but a less abrupt slackening of the growth rate with age, so that eventually the size attained is often greater than under accelerating conditions.

Similarly, the addition of somites, which is practically synonymous with the growth of the embryo, proceeds

faster under accelerating than under retarding conditions of development, but terminates relatively sooner and more abruptly. As a consequence, warm or brackish water forms of a species of fish have as a general rule fewer vertebrae than the forms inhabiting cooler or more saline water. An increase in the number of segments is also associated with protracted development having a basis in a great increase in the amount of yolk in the egg or in the larval-postlarval modification to pelagic life in which the muscle is replaced by gelatinous tissue.

Fishes passing through a protracted development often show an extenuation of age differentiation in form as well as of growth. Their proportions depart more from the juvenile conditions than do those of fishes going through a more hurried development. They often show also an increase in dermal modifications, as cirri, plates and spines. This increase in differentiation is more than proportionate to the extenuation of growth; at comparable sizes, the fishes passing through the contrasting types of development show these differences. The action of differentiation controls (inhibitions) is obviously hastened and accentuated under acceleration conditions.

Some supposedly contradictory cases are shown to be based on erroneous observations. Others, however, are valid, but can not be explained at present.

The problem of adaptation.—The modifications of developmental rate entailing definitive structural consequences seem best interpretable as physiological adaptations. When genetic, the changes in developing rate may be regarded as due to the selection of metabolic mutations, or to egg or larval modifications. Many of these structural consequences of physiological adaptations are among those characters of high systematic value long thought to be specifically devoid of adaptational significance. The rôle of adaptation in evolution is probably more extensive than has generally been postulated.

The problem of speciation.—The structural consequences of differential rate of development probably com-

prise a considerable proportion of the characters differentiating local races of fishes.

The problem of degeneration.—Degeneration resulting from accelerated development consists merely in the retention of juvenile characters. Degeneration correlated with decreased physiological activity and retarded development may be much more extensive, involving the elimination of final stages of *early* development and the retention of embryonic as contrasted with juvenile characters.

The problem of progressive evolution.—Accelerated development results in the emphasis of early differentiations, and seems to provide a means for the fixation and perpetuation of variations leading toward specialization.

The problems of phylogeny.—The interpretation of degeneration being associated with protracted development offers a means of testing whether simplicity of structure is a primitive or secondary feature. The general interpretations of the paper indicate that structural evolution controlled by alterations in developmental metabolism is approximately or even exactly reversible. Such changes involve particularly modifications of the adult toward or away from juvenile characteristics. If such changes are reversible, as seems highly probable, then the biogenetic law does not apply.

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